JOURNAL
OF THE
WASHINGTON ACADEMY OF SCIENCES

VOL. 43 January 1953 No. 1

PALEONTOLOGY.—*The classification of the strophomenoid brachiopods.* ALWYN WILLIAMS, Glasgow University. (Communicated by G. A. Cooper.)

The strophomenoid brachiopods include a host of diversified stocks that flourished mainly during Paleozoic times, although a descendant, the thecideid *Lacazella*, still survives. The morphological variation of the group is extremely wide, as a comparison of such bizarre forms as *Gemmellaroia*, *Leangella*, *Scacchinella*, *Stropheodonta*, *Thecospira*, and *Taffia* shows. Nevertheless, there are a number of morphological features that may be regarded as typically strophomenoid; they include the pseudopunctate condition of the test, the shell modification due to the loss of a functional pedicle, the presence of a pseudodeltidium and chilidium, the nature of the cardinal process and the absence of brachiophores, and shell convexity.

The pseudopunctae represent long, unbranched, arcuate calcareous rods embedded within the fibrous layer of the shell (Fig. 1). They do not penetrate the lamellar layer, and it is supposed that they were laid down by the outer epithelial layer of the mantle immediately behind the outer lobe. It is probable that the deposition and growth of these spicules were limited mainly to the mantle proper, for in the posteromedian portion of the adult shell, an area presumed to have been occupied by the viscera, an inner impunctate fibrous layer generally extends over a pseudopunctate zone laid down during the early stages of shell growth. In addition, the structures grouped around the notothyrium—the cardinal process, socket ridges, and notothyrial platform—are impunctate, as are also the teeth and supporting lamellae of the pedicle valve; although in the stropheodontids, which had a series of denticles arranged along the hinge-line in place of simple teeth each denticle is built of fibrous material deposited around a rod of nonfibrous calcite similar to the pseudopunctae. The chilidium and pseudodeltidium are also impunctate, being composed principally of an extension of the lamellar layer sometimes supported by an underlying deposit of fibrous calcite. Beecher (1901), p. 260) cited the impunctate nature of the pseudodeltidium as evidence to support his contention that the pseudodeltidium represents a third shell subsequently fused to the pedicle valve in contrast to the punctate deltidium, which he regarded as an integral part of the pedicle valve, in punctate telotrematous forms. In this respect at least his observations are incorrect: the pseudodeltidium is impunctate because it is composed of the lamellar layer which is not perforated in any strophomenoids, whereas the deltidium of such a form as a terebratuloid is punctate because both fibrous and lamellar layers of the shell are penetrated by the caecae.

It has long been known that in the postnepionic stages of the majority of strophomenoids a functional pedicle was absent and that consequently the mode of life varied from lying free on the sea floor to attachment either by the pedicle or by cementation of the pedicle valve to some foreign body. The persistence of a functional pedicle throughout life is more characteristic of the earlier strophomenoids for, despite exceptions like *Leptaena*, most of the later Lower Paleozoic stocks were not attached. Attachment by cementation of the pedicle valve was a later development attained by many independent groups but especially characteristic of the Upper Paleozoic orthotetaceids.

The position of the pedicle in relation to

the valves is a highly distinctive feature of the strophomenoids. In the young stages of unattached stocks like *Sowerbyella*, *Fardenia*, and *Strophomena*, as well as in forms with a persistently functional pedicle like *Leptaena*, the pedicle base was ensheathed in a pipe consisting of an extension of the lamellar layer situated on the apex of the umbo and not on any part of the interarea of the pedicle valve. This pedicle sheath then was distinct from the pseudodeltidium or delthyrium as can be seen in adult forms with the scar of the pedicle sheath still visible, though in some strophomenoids with a persistent pedicle the foramen was frequently enlarged by resorption and encroached on to the apex of the pseudodeltidium.

The disposition of the pedicle sheath represents a radical departure from the telotrematous pedicle opening which is limited to the delthyrium. Also if Percival's observation (1945) on *Terebratella inconspicua* Sowerby—that the pedicle valve occupies a dorsal position during development—had general application the position of the pedicle foramen has an added significance, for the inclination of the sheath away from the hinge-line suggests that in this group the converse was true.

The limitation of the pedicle opening to the apex of the pedicle valve and not to the interarea probably accounted for the complementary growth of the pseudodeltidium and chilidium: the latter structure is an integral part of the brachial valve yet it fits snugly with the edge of the former and its size is inversely proportional to the development of the pseudodeltidium. In this way the median openings of the interareas which in other brachiopods accommodated the pedicle were effectively sealed by the mantle flaps which were also responsible for the growth of the interareas. This complementary growth of the pseudodeltidium and chilidium was expressed in the more advanced stocks such as the strophedontids and orthotetaceids in a trend toward the complete elimination of the chilidium and the development of an entire pseudodeltidium flush with the hinge-line. This ultimate stage was reached independently by many Devonian strophedontids but only by one orthotetaceid, the Triassic *Thecospira*, for even in the Permian forms like *Meekella* and *Derbyia* a vestige of the chilidium remained and the pseudodeltidium carried a narrow median fold which accommodated it. Nevertheless, despite such a trend and its culmination in the strophedontids and *Thecospira* it is true to say that both structures are typical features of strophomenoid organization.

The development of two distinctive types of cardinal processes is also highly significant in the strophomenoids.

In a number of early stocks like *Taffia* and *Leptella* the diductor scars must have been attached directly to the floor of the notothyrium for there are no outgrowths which could have accommodated the muscle bases.

The most primitive modification of this state was the growth of a median partition which usually extended from the notothyrial floor to the chilidium as in the plectambonitids. This septum is commonly described as a simple cardinal process and the continued usage of this term is eminently convenient but in all probability the diductor bases were attached to the notothyrial floor on either side of the median septum or to a pair of small lateral ridges.

A similar development occurred in the leptestiids. Thus some early members like *Leptella* were without a median partition while some later stocks like *Leangella* were equipped with a series of lateral ridges in addition to the median septum. The leptestiids were characterized especially by the development of a pair of prominent plates—the chilidial plates—forming the lateral walls of the notothyrium. These together with the median septum were not only firmly ankylosed to the notothyrial floor but also elevated above the hinge-line and prolonged ventrally to it and since the muscle bases were probably inserted within the slots formed by the median septum and the chilidial plates the entire structure is analogous to the bilobed cardinal process.

The bilobed cardinal process of the strophomenaceids and orthotetaceids is quite distinct from the plectambonitaceid arrangement for the diductor muscles were attached not to the notothyrial floor but to a pair of outgrowths from it, each of which bore

the muscle bases on the posterior face, the area of attachment being often increased by the growth of numerous thin calcareous plates. Öpik (1932, p. 61) has commented on the presence of a fine ridge lying medianly between the lobes of the cardinal process of many strophomenaceids and his suggestion that this ridge is a degenerate homologue of the plectambonaceid median partition is probably true.

Despite subsequent modification of the strophomenaceid cardinal process, as for example the stropheodontids and orthotetaceids in which the chilidium and notothyrium are vestigial or absent and the cardinal process lobes project for some distance into the umbonal region of the pedicle valve, the pattern of development outlined above seems to be fundamental.

Another important feature of strophomenoid organization was the apparent, and in many stocks the undoubted, absence of

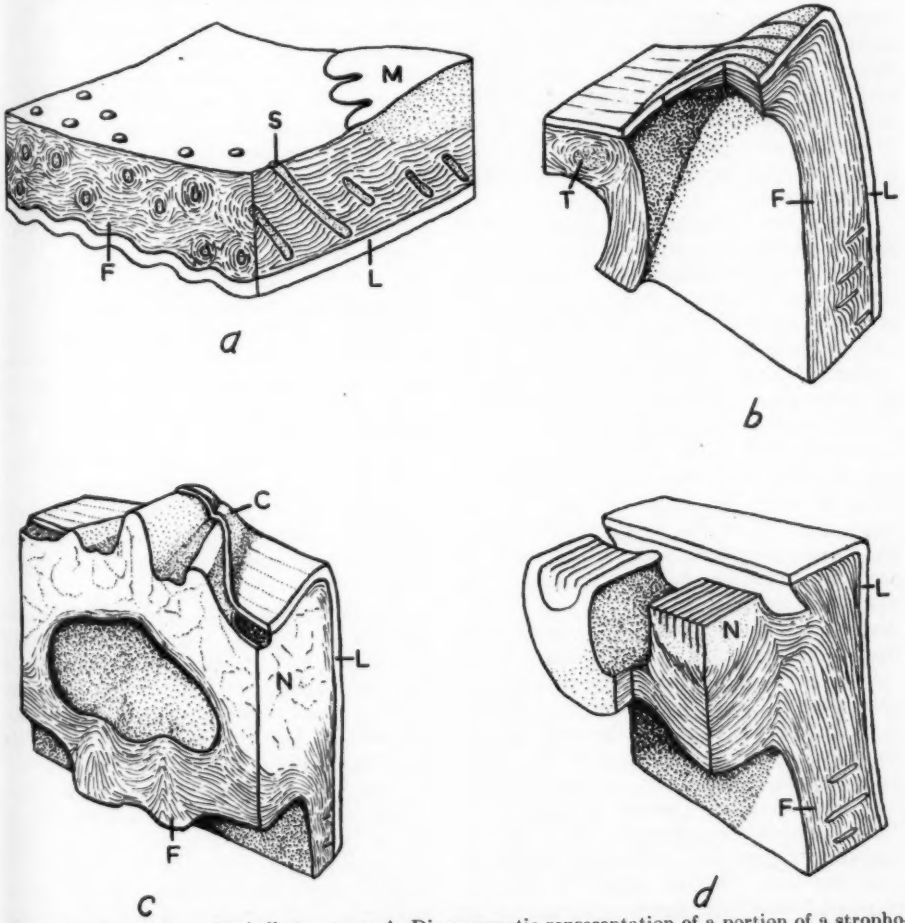


FIG. 1.—Strophomenoid shell structure: A, Diagrammatic representation of a portion of a strophomenoid valve just anterior to the muscle scar showing the lamellar layer (L), the spicules (S) embedded in the fibrous layer (F), and the nonfibrous calcareous deposit of the muscle base (M); B, structure of the strophomenoid pseudodeltidium showing the lamellar layer (L), the fibrous layer (F), and a section of a tooth (T); C and D, the plectambonaceid and strophomenaceid cardinal processes, as typified by *Sowerbyella* and *Strophonelloides*, respectively; chilidium (C), lamellar layer (L), fibrous layer (F), and calcareous nonfibrous deposit (N).

any specialized structures associated with the cardinalia which gave support to the lophophore. Thus in the strophеodontids the pair of ridges forming the inner boundary of the sockets in early members are usually referred to as "brachiophores." With the progressive spread of denticles along the hinge line in later stocks, the teeth and socket arrangement became vestigial and the ridges either disappear entirely or, exceptionally as in the Leptostrophias, became modified to form ankylosed buttresses to the cardinal process lobes. It seems then that the ridges were nothing more than internal walls to the sockets, and the function of lophophore support cannot be ascribed to them. This is equally true for the strophomenids which are equipped with weak ridges like the early strophеodontids.

Within the orthotetaceid group there is also no evidence to suggest that any specialized structures supported the lophophore; the presence of strong, large teeth, the loss of the interarea of the convex brachial valve, and the pronounced ventral growth of the bilobed cardinal process all contributed to the development of a pair of highly modified socket ridges which usually formed concave cups ankylosed to the sides of the cardinal process lobes and supported by a pair of plates growing up from the floor of the valve, e.g., *Meekella*. Even in *Thecospira* the calcareous spires were not attached to any structures associated with the socket ridges but were supported by a pair of very short, scarcely differentiated outgrowths from the bases of the cardinal process lobes.

Öpik (1933, p. 44) has come to a similar conclusion in his investigation of *Leangella* in which the ridges defining the teeth sockets are especially prominent; and in the plectambonaceids generally it is highly likely that the so-called "crural processes" or "brachiophores" functioned only as socket bounding ridges. It is therefore suggested that the term "socket ridge" be used in place of "crura" or "brachiophores" for all strophomenoids.

There is not very much evidence as to the form of the strophomenaceid lophophore but from a knowledge of occasionally preserved impressions as in *Leptaenisca* and *"Strophomena" jukesi* Davidson it is probable that it consisted of a pair of depressed spiral coils, a disposition compatible with shell configuration.

A spirolophous lophophore was apparently also characteristic of the orthotetaceids; impressions of depressed coiled brachia are found in *Davidsonia* and in *Thecospira*, a form hitherto classified as a rostrospiraceid, the fleshy brachia were strengthened by the development of a pair of spirally coiled calcareous ribbons. These spires form a pair of high cones extending well into the interior of the pedicle valve and it is probable that the lophophore of those orthotetaceids in which the depth of the shell was greatly increased by the exceptional growth of the pedicle valve were similarly disposed.

On the other hand many paleontologists, notably Kozlowski (1929) and Öpik (1933), have concluded that the strongly elevated and striated ridge often found in the plectambonaceid brachial valve completely surrounding the postero-median area (here called the "lophophore platform") represent the zone of attachment for the lophophore in a manner analogous to the lophophore-supporting structure of thecideids. The suggestion is certainly the most plausible explanation for the development of such an extraordinary feature and if it is correct the lophophore probably consisted of a simple lobate ring (compare the ptycholophous condition as in *Lacazella*).

Elevated ridges are also found in the brachial valve of the strophomenaceid *Christiania* and are strongly reminiscent of the plectambonaceid lophophore platform. In this stock however the partitions are disposed in two discrete loops and if the functional interpretation of these structures is correct the lophophore was schizolophous.

One other important characteristic remains to be discussed—namely, the configuration of the shell. The protegulum and nepionic shells of all strophomenoids, as far as known, were biconvex, a relationship that was maintained throughout the ontogeny of the orthotetaceids except for a minority like some schellwienellas in which the pedicle valve became concave during ephebic stages of growth.

The brachial valve of all strophomenaceids and plectambonaceids in contrast became concave in neanic stages at least and although many independent stocks develop resupinate shells the concavo-convex relationship of the neanic stage was never completely eliminated.

This contrast between the biconvex shell of the orthotetaceids and what is essentially a simple or modified concavo-convex shell of the plectambonaceids and strophomenaceids was probably accompanied by important differences in anatomical distribution and constituted a significant divergence within the group.

THE BASIS OF CLASSIFICATION

Until the publication of Öpik's brachiopod studies (1930–1934) the classification of the strophomenoids had never been in a satisfactory state although their distinctiveness had been apparent to paleontologists since 1848 when King took what was then a radical step and erected a family, the Strophomenidae, for the inclusion of *Strophomena* and allied forms. Even the historic studies of Beecher did little to stimulate any worthwhile suprageneric grouping and as recently as 1929 Schuchert and Le Vene (p. 16) described the classification of the strophomenoids as "not yet satisfactory" and were content to use resupination as a subfamily division of the Strophomenidae though they must have been aware of the artificiality of such an arrangement.

The plectambonaceid classification proposed by Öpik is preeminently utilitarian; it consists of the grouping together of demonstrably related genera into subfamilies, families, etc., by purely morphological comparisons: but because it is executed with all due regard to the range of individual stocks it transcends the pigeonholing of genera and allows for the establishment of as natural a classification as one can expect in the light of present knowledge.

The building up of a classification from a series of basic units in this way reveals a number of important features concerning the morphogeny of a series of related stocks. It is for instance usual to find that very few, if any, characters are peculiar to a group; many characters, often the most diagnostic ones, appear independently in other remotely related stocks and it appears that the higher the suprageneric category the greater the morphological overlap with other categories.

Thus superfamily definitions of plectambonitaceids and the orthoid clitambonaceids classified in this way are virtually the same although nobody acquainted with the groups would hesitate to agree that they were independent of each other from inception to extinction.

This continual reduplication of morphological features in undoubtedly independent groups is of course related to the mechanics of evolution. It is an expression of parallelism in related stocks and though it raises many taxonomic problems it cannot be ignored. This realization should allay most doubts arising from a classification in which it is sometimes impossible to describe a series of characters which are unique to one category or another.

Another fact emerging from the building up of a classification by the grouping together of related genera is that any morphological features will generally have a taxonomic importance directly related to the number of independent lines of descent (expressed systematically as genera) constituting a stock and not a preconceived value constant throughout a series of stocks. For example, the type of cardinal process is taxonomically one of the most important strophomenoid characters. Along with other features it serves to distinguish the plectambonitaceids from the strophomenaceids and in this instance has a superfamily status. In contrast, the absence of a cardinal process in the taffiids and leptestiids serves only to distinguish genera although had such primitive stocks undergone persistent divergences and specialization unaccompanied by the development of a cardinal process its absence would have been correspondingly more important taxonomically.

This is true for instance of the orthotetaceids. The orthotetaceids were equipped with a bilobed cardinal process homologous with the strophomenaceid one, and on the basis of this structure alone would be included within the strophomenaceids. But

the orthotetaceid stock, which was distinct in such features as the persistence of a biconvex shell throughout ontogeny and the almost universal adoption of the cementing habit, survived into the Trias and during its existence underwent a number of significant divergences some of which merit family recognition, thus imparting to the stock a superfamily status. Accordingly the bilobed cardinal process being present in all members of the Strophomenacea and Orthotetacea has a subordinal value.

This pattern of variable taxonomic values for the cardinal process is true for all characters and is a natural manifestation of divergence and development.

The classification proposed below has been modelled with the foregoing considerations in mind. Its basic units—the generic stocks—have been grouped together into appropriate suprageneric categories and the only factor other than morphological comparison which has been given particular attention is the time range of each genus, in the hope that the more blatant deficiencies of morphological grouping will be eliminated.

Suborder STROPHOMENOIDEA Öpik, 1934, emended

Brachiopods derived out of orthoid ancestors by the development of a pseudopunctate shell and by the early loss of a functional pedicle so that the majority of forms included in the suborder either lay free on the sea floor or were attached by cementation to a foreign body; delthyrium and notothyrium closed posteriorly by the complementary development of a pseudodeltidium and chilidium; diductor bases of the branchial valve attached to a bilobed cardinal process or to the notothyrial floor variously modified and usually divided into two distinct areas by a median "cardianal process"; lophophore, unsupported by any specialized part of the cardinalia but in some stocks presumably attached to a platform developed on the brachial valve and exceptionally strengthened by a calcareous skeleton, generally spirolophous, sometimes ptycholophous, exceptionally schizolophous. Lower Ordovician to Recent.

PLECTAMBONACEA, n. superfamily

Concavo-convex or resupinate strophomenoids with cardinalia consisting of well developed socket ridges, a notothyrium covered by a convex chilidium sometimes supported, and exceptionally replaced, by a pair of chilidial plates, and a cardinal process, which when present, consists of a simple median ridge with subsidiary lateral ridges in later forms; pseudodeltidium small, pedicle presumably functional in those adult forms with a persistent supra-apical foramen, more usually lost during ontogeny so that mature shells of most stocks were unattached. Ordovician to Devonian.

Family Taffiidae Ulrich and Cooper, 1936

Plectambonaceids with orthoidlike musculature and cardinalia; notothyrium covered completely by a convex chilidium, cardinal process when present, simple, median supra-apical foramen small, persistent throughout ontogeny. Lower Ordovician, Upper Canadian to Chazy. Type genus, *Taffia* Ulrich.

Family Plectambonitidae Kozlowski, 1929

Plectambonaceids with a median cardinal process growing from the notothyrial floor and ankylosed posteriorly to a convex chilidium; pedicle valve with a pair of accessory teeth lying anterolaterally to two simple teeth; brachial valve with a variably developed lophophore platform; supra-apical foramen sporadically persistent in adult forms. Lower and Middle Ordovician.

Subfamily Plectambonitinae Jones, 1928

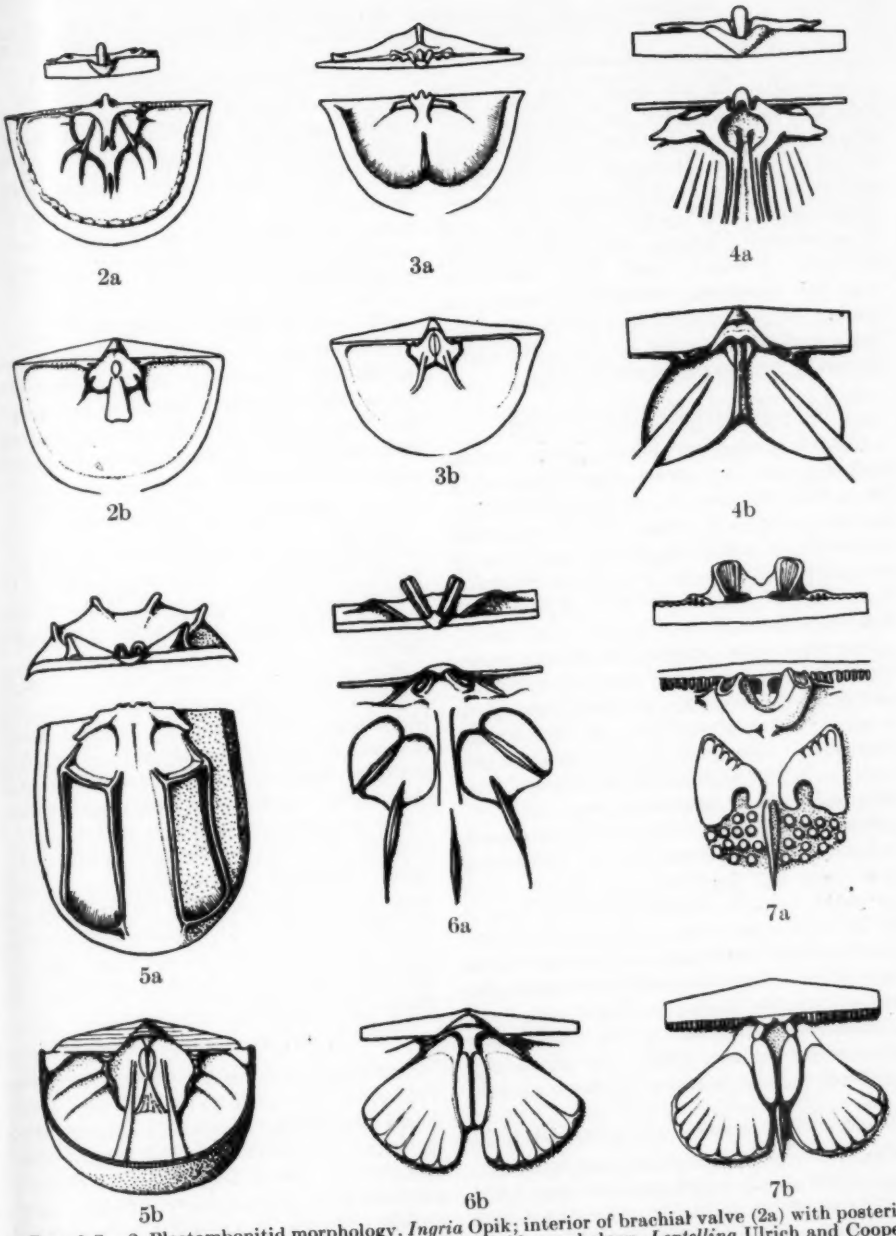
Plectambonitids with a denticulate hinge line in addition to the accessory and simple teeth; pedicle valve with divergent diductor scars separated anteriorly by a low broad plate; brachial valve with aseptate muscle scars. Lower and Middle Ordovician (B_2 to C_3 of the Baltic.) Type genus, *Plectambonites* Pander.

Subfamily Ahtiellinae Öpik, 1933

Plectambonitids with smooth hinge lines and a lophophore platform developed on the brachial valve. Lower Ordovician (B_3 to C_1 of the Baltic.) Type genus, *Ahtiella* Öpik.

Leptestiidae, n. family

Plectambonaceids with a pair of chilidial plates usually supporting a chilidium forming the sides of the notothyrium and generally ankylosed to the median cardinal process to form a tripartite structure; brachial valve usually provided with an elevated lophophore platform. Lower Ordovician to Middle Devonian.



FIGS. 2–7.—2, Plectambonitid morphology, *Ingria* Opik; interior of brachial valve (2a) with posterior view above; interior of pedicle valve (2b). 3, Leptestiinid morphology, *Leptellina* Ulrich and Cooper; interior of brachial valve (3a) with posterior view above; interior of pedicle valve (3b). 4, Sowerbyellinid morphology as typified by *Sowerbyella* Jones; cardinalia of brachial valve (4a) with posterior view above, posteromedian area of pedicle valve (4b). 5, Christianiid morphology as typified by *Christiania* Hall and Clarke; interior of brachial valve (5a) with posterior view above, interior of pedicle valve (5b) with the anterior part of the shell removed to show the posteromedian area. 6, Generalized strophomenid morphology; cardinalia and muscle scars of brachial valve (6a) with posterior view above, posteromedian area of pedicle valve interior (6b). 7, Stropheodontid morphology, *Strophonelloides* Caster; cardinalia and muscle scars of brachial valve (7a) with posterior view above, posteromedian area of pedicle valve interior (7b).

Subfamily Leptestiinae Öpik, 1933

Leptestiids with the socket ridges not fused with the chilidial plates and with a strongly developed lophophore platform; median cardinal process occasionally absent, in some later stocks flanked by two or more subsidiary ridges; adductor scars of brachial valve sometimes borne on an elevated platform lying anterior to the cardinalia; accessory teeth and denticulate hinge-line occasionally developed; supraapical foramen never persistent throughout ontogeny. Lower Ordovician (Upper Canadian) to Upper Silurian. Type genus, *Leptestia* Bekker.

Subfamily Sowerbyellinae Öpik, 1930

Leptestiids with the chilidial plates, median cardinal process, and socket ridges ankylosed to the notothyrial platform to give a structure like an inverted V; hinge line exceptionally denticulate or pierced by oblique canals; apical foramen rarely persistent throughout ontogeny. Ordovician to Middle Devonian. Type genus, *Sowerbyella* Jones.

Discussion.—The leptestiinids and the sowerbyellinids were from their inception quite distinct from contemporary plectambonaceids especially in the development of the chilidial plates and it seems that the two groups represented an important divergent development from the strophomenoid ancestral stocks.

Ulrich and Cooper (1936, p. 626) erected a subfamily, the Leptellinae, for the inclusion of early forms like *Leptellina* and *Leptella* which had either a simple cardinal process or none at all. In the opinion of the writer the subfamily is best regarded as a synonym of the Leptestiinae Öpik, 1933; many European leptestiinids also possess a simple median cardinal process and its absence in *Leptella* was, as Ulrich and Cooper demonstrated for the taffiids, not particularly significant among primitive plectambonaceids.

Superfamily STROPHOMENACEA Schuchert, 1896

Concavo-convex or resupinate, pseudopunctate brachiopods usually with a persistent supraapical foramen which became sealed up by shell deposit in some later stocks so that mature individuals were either unattached or, exceptionally, cemented by part of the pedicle valve to a foreign body; cardinal process bilobed; pseudodeltidium sometimes completely closing the delthyrium, chilidium when present consisting of a simple convex arch. Ordovician to Carboniferous.

Family Strophomenidae King, 1846

Strophomenaceids with a pair of simple teeth usually supported by small dental lamellae; pseudodeltidium never completely closing the delthyrium, chilidium always present; brachia lacking skeletal support but apparently consisting of a pair of very low spires exceptionally impressed on the internal shell surface. Ordovician to Carboniferous.

Strophomeninae, n. subfamily

Strophomenids usually with a functional pedicle throughout ontogeny but sometimes lying free on the substratum due to the sealing up of the supra-apical foramen during maturity Ordovician to Carboniferous. Type genus, *Strophomena* de Blainville.

Leptaenoideinae, n. subfamily

Strophomenids attached throughout ontogeny by the cementation of the umbonal region of the pedicle valve to a foreign body. Middle Silurian to Lower Devonian. Type genus, *Leptaenoidea* Hedström.

Discussion.—The proposed family Rafinesquinidae Caster (1939) is synonymous with Strophomenidae King, 1846, as emended above. The only way to continue recognizing both families is to relegate all resupinate forms to the Strophomenidae, a patently artificial discrimination.

The adoption of secondary attachment by cementation in two strophomenid stocks (*Leptaenoidea* Hedström and *Leptaenisca* Beecher) seems to merit the division of the strophomenids into two new subfamilies. Cementation constituted a profound change of habit and was also achieved independently of this development by other strophomenoids.

Family Stropheodontidae Caster, 1939

Strophomenaceids lacking a functional pedicle with the simple teeth and dental lamellae replaced by denticles subsequently spreading along the hinge-line; socket ridges abbreviated subsequent to the loss of dental lamellae becoming obsolescent or disappearing completely, exceptionally forming buttresses to the cardinal process lobes; pseudodeltidium initially small, apical, becoming progressively larger and in some stocks ultimately closing the delthyrium completely; chilidium initially massive becoming degenerate and in some stocks ultimately completely lost. Upper Ordovician to Upper Devonian.

Subfamily Stropheodontinae Caster, 1939

Stropheodontids which lay free on the substratum during maturity. Upper Ordovician to Upper Devonian. Type genus, *Stropheodonta* Hall.

Liljevallinae, n. subfamily

Stropheodontids which were attached throughout ontogeny by cementation of the pedicle valve to a foreign body. Middle Silurian. Type genus, *Liljevallia* Hedström.

Discussion.—The stropheodontid affinities of *Liljevallia* are revealed in the development of denticles along the hinge-line on either side of the delthyrium, the absence of dental lamellae and simple teeth, and the brachyprionid muscle scar. The stock, then, like the leptaenoideinids and the orthotetaceids is illustrative of the development of cemented forms from a number of unattached independent strophomenoid ancestors. Hitherto *Liljevallia*, *Leptaenoidea*, and *Leptaenisca* have usually been placed within the Davidsoniinae but each genus has pronounced affinities with either the Strophomenidae or the Stropheodontidae and it seems better to erect new subfamilies in the manner proposed above than to continue previous practice.

Christianiidae, n. family

Concavo-convex strophomenaceids with a lophophore platform consisting of a pair of discrete, U-shaped loops presumably giving support to a schizolophous lophophore; pseudodeltidium and convex chilidium well developed, cardinal process bilobed, socket ridges strong; supra-apical foramen persistent throughout ontogeny. Middle and Upper Ordovician Type genus, *Christiania* Hall and Clarke.

Discussion.—*Christiania* represents an isolated terminal development out of one of the early strophomenoid divergences which is not closely related to any other known stock. The presence of a lophophore platform suggests affinities with the Plectambonacea, but it is more probable that the platform, which is not like any plectambonaceid structure, represents an independent convergent development for in other respects and especially in the possession of a bilobed cardinal process *Christiania* is strophomenaceid.

ORTHOTETACEA, n. superfamily

Strophomenoids without a functional pedicle; pedicle valve usually greatly modified and cemented by the umbo or a greater part of the shell surface to a foreign body; brachial valve convex throughout ontogeny; cardinal process bilobed often greatly extended into the pedicle valve, sometimes highly modified; lophophore probably spirolophous in all stocks, exceptionally impressed and supported by spirally coiled calcareous ribbons. Upper Ordovician to Triassic.

Family Orthotetidae MacEwan, 1939

Orthotetaceids with a variable but well developed hinge-line and interarea in the pedicle valve; pedicle valve consisting of one continuous chamber; pseudodeltidium of earlier stocks apical and chilidium correspondingly massive, in later stocks pseudodeltidium completely covering delthyrium, chilidium vestigial, perideltidium always present; shell surface usually finely costellate with additional radial plicae in many later stocks. Upper Ordovician to Permian.

Subfamily Orthotetinae Waagen, 1884

Orthotetids equipped with a pair of dental lamellae often extravagantly developed and in various stages of convergence and coalescence. Upper Ordovician to Permian. Type genus, *Orthotetes* Fischer.

Schuchertellinae, n. subfamily

Orthotetids which have lost the dental lamellae through obsolescence. Devonian to Permian. Type genus, *Schuchertella* Girty.

Subfamily Davidsoniinae King, 1850·

Orthotetids lacking costellate ornamentation; pseudodeltidium and chilidium well developed; dental lamellae obsolescent, sockets deep bounded by flaring socket ridges fused with cardinal process; both valves bear the impressions of a pair of spirally coiled brachia forming very ow cones with the apices directed towards the brachial valve. Middle Devonian. Type genus, *Davidsonia* Bouchard.

Discussion.—The term perideltidium (Dunbar and Condra 1932, p. 67): has been given to a pair of triangular surfaces forming part of the interarea of the orthotetid pedicle valve and lying lateral to the pseudodeltidium although not necessarily adjacent to it. The perideltidium is variable in area and development but is an integral part of the interarea and is not an occurrence dependent on shell exfoliation.

Each area is slightly elevated above the rest of the interarea and in addition to being orna-

mented by growth lines parallel to the hinge-line is also feebly striated at right angles to the hinge-line so that the resultant series of grooves and ridges does not radiate from the umbo and lie obliquely to the perideltidial boundaries. Serial sections of a number of orthotetids substantiate the conclusions of Dunbar and Condra that the perideltidial boundaries are represented by a sharp deflection of both lamellar and fibrous layers. It can also be observed that the striations represent crenulations of the lamellar layer and that part of the fibrous layer adjacent to it. One would have anticipated constrictions on the hinge-line of the brachial valve corresponding to the deflected edges of the perideltidium, but none can be observed, and no plausible reason can be suggested for this differentiation of the interarea.

Apart from including the Davidsoniinae within the Orthotetidae the division of the family into two subfamilies dependent upon the presence or absence of dental lamellae is, in the opinion of the writer, more than a convenient morphological grouping for it seems to have been one of the natural consequences of orthotetid development.

The earliest known orthotetid, *Fardenia* Lamont, a biconvex form equipped with dental lamellae, appeared towards the end of the Ordovician and flourished throughout the Silurian. There is evidence to suggest (Williams, 1950, p. 120) that by the end of Silurian times sufficient divergence had occurred within the stock to give rise to a schuchertellid, which had lost the dental lamellae by obsolescence, and also a concavo-convex Schellwienella (like the Lower Devonian *S. umbraculum* (Schloth.)) with strongly developed divergent dental lamellae.

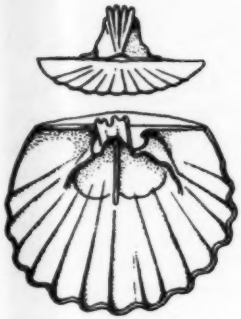
It is probable that two such forms were ancestral to two main stocks, viz, orthotetinid and schuchertellinid which remained independent during their subsequent histories. The range of all described genera is consistent with this belief and there is no evidence to suggest that either stock was replenished from the other by obsolescence of the dental lamellae or the development of secondary ones.

With regard to the various genera equipped with well-developed dental lamellae it is noteworthy that the disposition of the lamellae seems to be closely related to the configuration of the pedicle valve. Thus Schellwienellas possess concave pedicle valves and divergent dental lamellae while all other orthotetinids have convex pedicle valves and dental lamellae which are parallel, convergent, or in various stages of coalescence. Taking into consideration the fact that the dental lamellae always occupied a constant position relative to the interarea, where they lay immediately beneath the teeth, it is reasonable to assume that their disposition was a function of the form and growth of the anterior wall of the pedicle valve. Consequently many species ascribed to such genera as *Sicelia*, *Orthotetina*, *Geyerella*, and *Meekella* may represent independent convergences rather than closely related stocks.

Gemmellaroiidae, n. family

Attached orthotetaceids with a long conical pedicle valve capped by a reduced operculiform brachial valve; hinge-line obsolescent, interarea completely lost except for a narrow elevated ridge in the pedicle valve representing the pseudodeltidium; articulation aided by the development in both valves of an excessively thickened margin serrated by oblique furrows; cardinalia massive, elongated, with the bilobed cardinal process and laterally extended socket ridges completely fused, in the interior of the pedicle valve the cardinalia is contained within a subcircular myophore chamber, about a third the length of the valve extending from the umbo almost to the periphery of the valve and lying immediately anterior to the pseudodeltidium; fibrous layer of shell adjacent to lamellar layer disposed in long sharp folds radiating from the umbo. Permian. Type genus *Gemmellaroia* Crossman.

FIGS. 8–12.—8, Orthotetinid morphology, *Meekella* White and St. John; interior of brachial valve (8a) with posterior view above; interior of pedicle valve (8b). 9, Scacchinellid morphology as typified by *Scacchinella* Gemmellaro; interior of brachial valve (9a); reconstruction of part of the pedicle valve interior (9b) showing the median septum and the transverse partitions. 10, Gemmellaroiid morphology as typified by *Gemmellaroia* Crossman; complete shell with a transverse section of the pedicle valve to show the shell structure and the disposition of the myophore chamber (10b), anterior view of brachial valve interior (10a). 11, Thecospirid morphology as typified by *Thecospira* Zugmayer; interior of brachial valve (11a), interior of pedicle valve (11b) tilted to show the muscle scar arrangement. 12, Diagrammatic representation of the interarea of the orthotetid pedicle valve to show the nature of the perideltidium (PE); lamellar layer (L), fibrous layer (F), pseudodeltidium (P), tooth (T).



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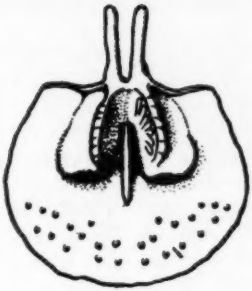

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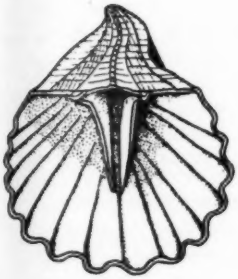

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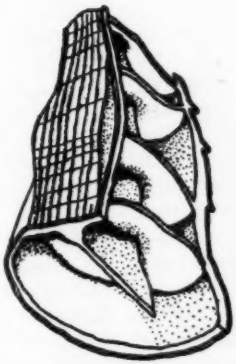

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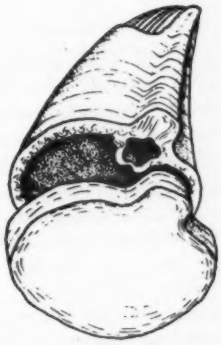

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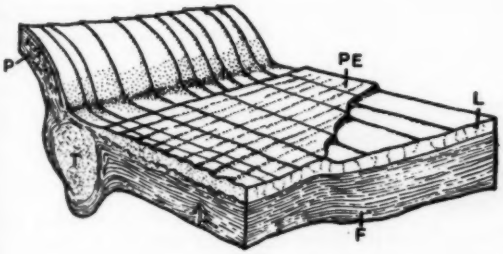

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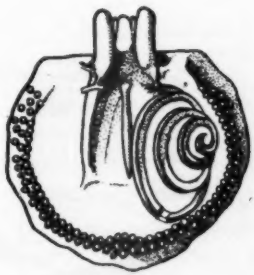
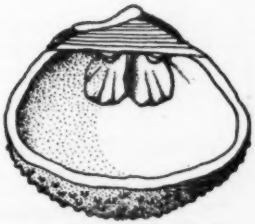


11a



11b

FIGS. 8–12 (See opposite page for legend).

Discussion.—The gemmellaroiids represent a later divergence from a more generalized orthotetid stock in which a number of morphological modifications present in the orthotetids generally are carried to conclusion. Thus the excessive elongation of the pedicle valve and the reduction of the hinge-line is seen in late orthotetids like *Orthotetina* but never on the scale of the gemmellaroiids. The myophore chamber is especially characteristic of the family but is not unique for a similar structure evolved in an otherwise typical Permian orthotetid (*Orthotetella* King).

Scacchinellidae, n. family

Attached orthotetaceids, pedicle valve long, conical twisted with longitudinally striated interarea, brachial valve gently convex, exterior spinose without radial ornamentation; interior of pedicle valve with a strong median septum extending anteriorly for over half the length of the shell and divided into a series of chambers by the deposition of a variable number of transverse partitions the last formed chamber presumably being the only one occupied by the viscera; brachial valve with a long bilobed cardinal process which extended well into the pedicle valve on either side of the median septum; socket ridges small, adductor muscle scars impressed on the inner surfaces of a pair of long, thick ridges extending anteriorly from the cardinal process bases. Permian. Type genus, *Scacchinella* Gemmellaro.

Discussion.—The scacchinellids are unique among the orthotetaceids and indeed among all brachiopods in the division of the pedicle valve into a series of chambers by the deposition of transverse partitions. The writer has observed in an occasional *Derbyia* the apparently natural occurrence of thin flaps of fibrous shell deposit projecting into the body chamber and a similar occurrence is reported by Licharew (1928, p. 272) in the gemmellaroiid *Tectarea*. But in the scacchinellids the partitions were apparently a regular feature of all mature individuals and were presumably a consequence of the great disparity between the volume of the soft parts and the excessive elongation of the pedicle valve.

Family Thecospiridae Bittner, 1893

Orthotetaceids attached to a foreign body by cementation of the pedicle valve, exterior tuberculate without radial ornamentation but sometimes rugate; interarea of pedicle valve entire, without any definition of the pseudodeltidium, interarea of brachial valve vestigial,

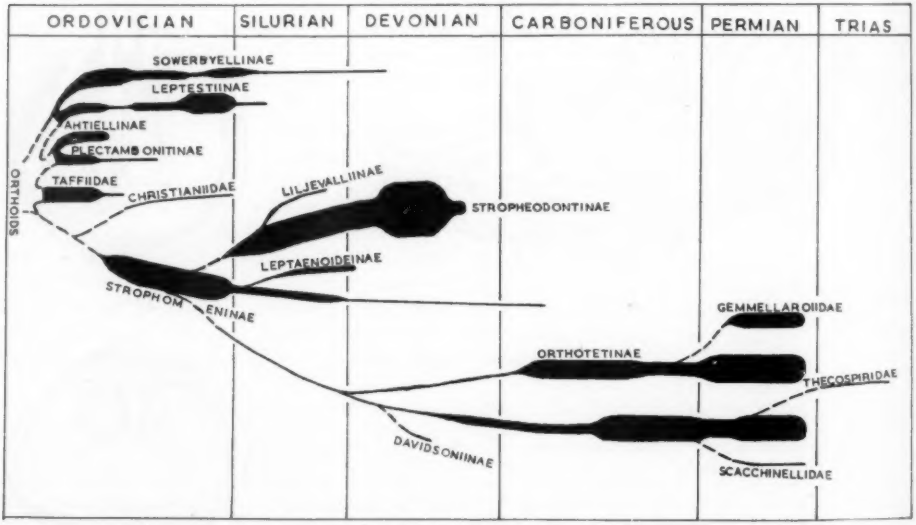


FIG. 13.—The stratigraphical distribution of the strophomenoid brachiopods, including the thecideids; the size of the suprageneric categories figured in the chart is proportionate to the number of genera included in each category as well as their stratigraphical range.

childium absent; pedicle valve with strong unsupported teeth and a small broad muscle scar divided medianly by a low median septum; brachial valve with an erect cardinal process, functionally bilobed but united medianly to form a tripartite structure, sockets deep, muscle scars contained within a pair of subparallel ridges extending anteriorly from the cardinalia and divided medianly by a low median ridge; cardinal process bases prolonged into a pair of short processes which support a pair of spirally coiled calcareous ribbons directed towards the lateral slopes of the pedicle valve; brachial ribbon sharply folded throughout its length to give a V-shaped cross section. Triassic. Type genus, *Thecospira* Zugmayer.

Discussion.—The orthotetaceid features of *Thecospira* are so striking and numerous that it cannot be excluded from the strophomenoids because its lophophore was supported by a pair of spirally coiled calcareous ribbons. The shell is strongly pseudopunctate, the spicules penetrate the internal surfaces which are tuberculate and though they do not penetrate the lamellar layer they are excessively prolonged to give the exterior a bluntly spinose appearance. Other strophomenoid features include the mode of attachment, the entire interarea of the pedicle valve (compare the strophеodontids and a similar tendency in those orthotetaceids with a vestigial chilidium) the cardinal process and the muscle scars which are reminiscent of late orthotetaceids like *Derbya*.

The presence of calcified spiral supports in *Thecospira* then does not signify that the stock was related to the rostrospiroids or spiriferoids; they represent an independent development out of a spirolophous orthetetaceid.

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PALEOBOTANY. —Prosseria grandis, *a new genus and new species from the Upper Devonian of New York.*[1] CHARLES B. READ, U. S. Geological Survey. (Communicated by Roland W. Brown.)

The extensive collections of fossil plants made by C. S. Prosser from Devonian horizons in New York and Ohio contain numerous specimens of interest to students of Paleozoic floras. One of the most remarkable of these specimens is a large slab of black shale and its counterpart carrying as an incrustation the remains of an unusual representative of the Articulatae. The literature on Devonian floras contains no reference to any genus that may be extended to include this plant. In consequence this fossil is referred to a new genus, *Prosseria*, named in honor of the collector. There follows a discussion of the type specimen and its possible relationships.

PTERIDOPHYTA
Articulatae
?Pseudoborniales

Prosseria, n. gen.

Generic characters at present defined by the single known species.

Prosseria grandis, n. sp.

Diagnosis.—Plant large, stem 25 mm in di-

[1] Publication authorized by the Director, U. S. Geological Survey.

ameter in the type, articulate, surface smooth. Nodes enlarged (40–50 mm in diameter) and giving off both branches and whorls of leaves. Leaves about 18 (?), 9–11 visible on one side, apparently in fascicles of three, emerging from definite points of insertion at the node; linear and long (33 cm long and 6 mm wide), narrow at base and enlarging gradually upward for about 15 centimeters, nervation indistinct. Branches, 2 at each node, emerging from opposite sides of the stem, only the bases preserved in the type specimen.

Collected by C. S. Prosser in 1889 from the "Upper Genesee" shale (West River shale, Genesee group), Kimble Gully, 1 mile southeast of Penn Yan, Yates County, N. Y.

Discussion.—The general aspect of *Prosseria grandis* is shown in Fig. 1. The nearly smooth stem with enlarged nodes, the whorl of linear leaves, and the opposite branching are striking features of the fossil. The leaves, as has already been pointed out, are in fascicles of three on the one side exposed. Details of the lower portions of the leaves and of the bases are rather vague, however, and do not permit critical study. Judged from the occurrences of leaves attached only at the upper one of the two nodes and their absence in the lower node, the appendages must have developed definite abscission layers. It will be seen that there are three distinct leaf bases in the half of the flattened stem exposed at the upper node. These are circular, and leave a distinct impression, suggesting definite articulations by their clear-cut aspect as indicated above.

The two lateral organs at each node are obviously in a different category from the strap-shaped leaves. Their larger size, the open angle they make with the stem, and their frayed ends (indicative of the absence of an abscission layer) are proof of this. These are regarded by the writer as lateral branches.

With the meager data at hand concerning this fossil it is obviously unwise to attempt any estimate of the size of the entire plant. The plant may have been quite large, in which case the specimen is but a branch. On the other hand the plant very likely was a relatively small one, and the axis here preserved is the main shoot.

The affinities of *Prosseria grandis* are beyond question with the Articulatae. The plant may possibly be related to *Pseudobornia* Nathorst. The features observable in the material are, however, scarcely sufficient to be conclusive. It will be recalled that *Pseudobornia*[2] is characterized by large articulated stems with one to two branches at each node. The leaves are in whorls of four, are short-stalked, dichotomously divided, and with toothed margins. Their general aspect is somewhat plumose. The fructification is a strobilus said to be comparable with *Cheirostrobus* Scott.[3] The single well-known species, *Pseudobornia ursina* Nathorst, is from the Upper Devonian of Bear Island. This genus is an isolated type which, in the opinion of many paleobotanists, shows affinities with the *Sphenophyllales*. The linear leaves of *Prosseria* contrast strongly with the plumose ones of *Pseudobornia* and provide adequate grounds for generic separation. The stem provides little information of value in determining relationships, and, in the absence of fertile structures of *Prosseria*, it is obviously impossible to reach any definite conclusion regarding exact affinities.

There are likewise known the Middle Devonian *Calamophyton* and *Hyenia*, grouped by Krausel and Weyland in the Protoarticulatae. These plants, at least in their general makeup, are far more primitive types than *Prosseria*, showing only a semiverticillate arrangement of much smaller and definitely dichotomous leaves.

To the writer it would seem that *Prosseria* is much more closely related to the *Sphenophyllales* or *Pseudoborniales* than to the *Equisteales*. The greatly enlarged nodes of *Prosseria* certainly indicate this. Such a condition is quite characteristic of the stems of *Sphenophyllum*, common in the Carboniferous. Nathorst's figures of *Pseudobornia ursina* show the same condition. Stems of *Calamites* do not, however, show this.

Comparison with the stems identified by Dawson as *Calamites inornatus*[4] and later referred by White to *Pseudobornia*[5] is unsatisfactory. Dawson's plant is a broadly ribbed type with the nodes scarcely enlarged. The prominent nodal scars so characteristic of *Prosseria* are not shown

[2] NATHORST, A. G., *Zur fossilen Flora der Polarländer*. Kongl. Svenska Vet.-Akad. Handl. **36** (2): 25–28, pl. 7, figs. 9–13, pl. 8, figs. 1, 3–13, pl. 9, pl. 10, figs. 1–3. 1902.

[3] SCOTT, D. H., *On* Cheirostrobus, *a new type of fossil cone from the calciferous sandstone*. Philos. Trans. Roy. Soc. London **189**: ser. B, 1–34, pls. 1–6. 1897.

[4] DAWSON, J. W., *Flora of the Devonian period in northeastern America*. Quart. Journ. Geol. Soc. **18**: 310, pl. 17, fig. 56. 1862.

[5] WHITE, D. in Kindle, E. M., *Stratigraphic relations of Devonian shales of northern Ohio*. Amer. Journ. Sci. **34** (4): 210. 1912.

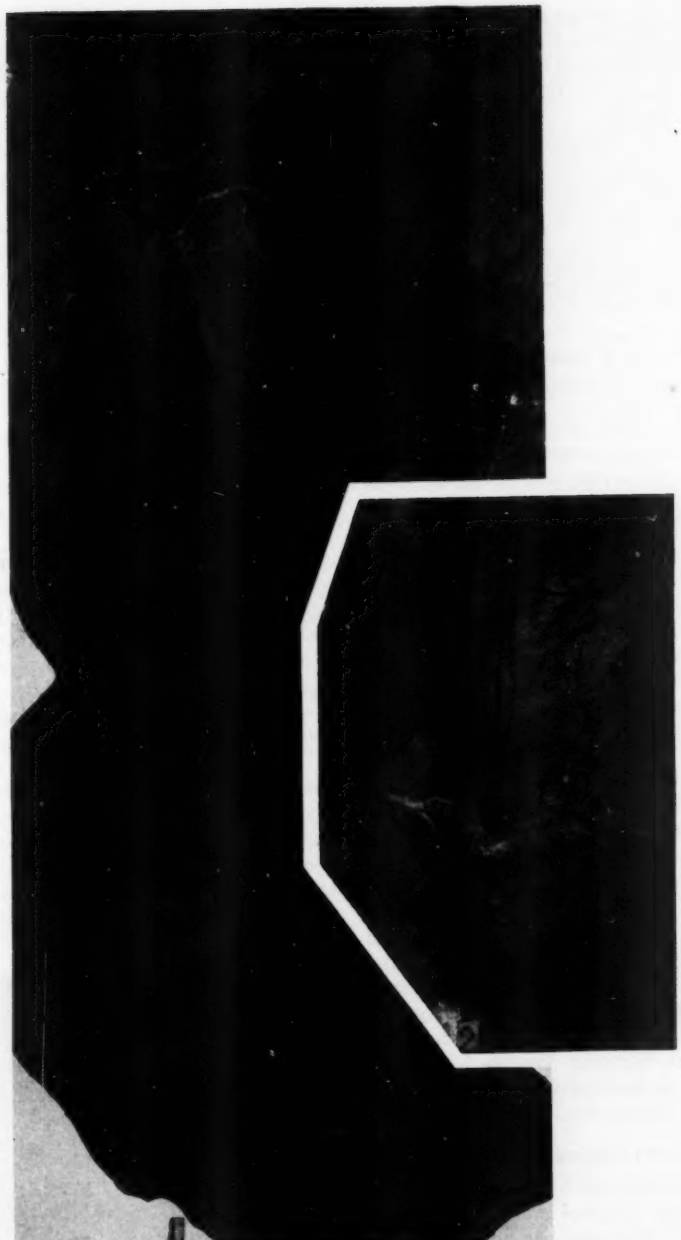


FIG. 1.—Photograph of the shale slab carrying the specimen of *Prosseria grandis*, showing the great length of the leaves, the enlarged nodes, and the smooth stem, × ½.

FIG. 2.—Photograph of the upper of the two nodes of the preceding figure showing the leaf bases and the opposite branch(?) bases, × 1.

in the figure of the type specimen of *C. inornatus*. It is, in fact, extremely doubtful if there is sufficient information available to permit the proper generic determination of the latter. It is quite likely a *Protocalamites*.

This new plant, although only its vegetative features are known and those imperfectly, has a rather important morphological significance. Briefly, *Prossera grandis* is an early member of the Articulatae of early Late Devonian age (Portage). It shows definite whorls of large and long-divided leaves. The nodal structure suggests affinity with the *Sphenophyllales*. The leaves are, however, far larger than those of the Carboniferous Articulatae. These large leaves in this very early type hardly support the frequent claims that the leaves of this group were originally microphyllous. Rather, the suggestion, based on arrangement of the known members of the Articulatae in chronologic order with *Prosseria* taking its place near, at least, to the base, is that the series may be one of reduction from megaphylls rather than expansion from microphylls.

MYCOLOGY.—*A new species of* Protodontia *from British Columbia*. G. W. Martin, State University of Iowa.

In January 1950 Dr. Ruth Macrae, of the Division of Botany and Plant Pathology, Department of Agriculture, Ottawa, Canada, sent me two specimens of a tremellaceous fungus, accompanied by careful notes and drawings, which obviously represented the same species but which were clearly distinct from any I had previously seen or to which I could find reference in the literature. Both had been collected the preceding year by W. G. Ziller on slash of black cottonwood in central British Columbia. The specimens, although sporulating freely, appeared to be incompletely developed and the assignment to a genus offered great difficulty, hence I laid them aside awaiting fuller information. Meanwhile, two additional collections from the same area were found in the collections at Ottawa, one collected by Mr. Ziller and one by Dr. M. K. Nobles. Dr. Macrae kindly sent me the balance of the material from Ottawa and Mr. Ziller let me see the even more abundant material of all four collections deposited in the Forest Pathology Collection of the Dominion Department of Agriculture at Victoria, British Columbia. On the basis of this material, I feel justified in describing the species.

Protodontia oligacantha, sp. nov.

Fructificationibus late effusis, resupinatis, tenuibus, mediis fuligineis vel avellaneis, ad fimbrias albas pallescentibus; aculeis sparsis, fimbriatis, albis, ad 0.6 mm longis; hymenio in basidiis et dendrophysibus dense aggregatis consistente; subhymenio hyalino; hyphis fundamenti fulvis; probasidiis globosis vel pyriformibus, plerumque 13–20 × 9–12μ, denique cruciatim-septatis; epibasidiis crassis breviculis latis, 2–2.5(–3)μ; basidiosporis cylindraceo-curvulis, apiculatis, (9–)10–12(–13) × (4–)4.5–5(–5.5)μ, per repetitionem germinantibus.

Broadly effused, up to 13 × 5 cm in extent, possibly larger, Benzo Brown to Cinnamon Drab, fading to buff or pallid near the broad, thin, fimbriate, white margin; waxy when moist, the hymenial surface drying horny; spines blunt, broad, somewhat fimbriate, white, up to 600μ long and 350μ in diameter at base, tapering toward tips, sparsely and irregularly distributed; in section 65–230μ thick between the spines, composed of a colorless hymenial layer 20–40μ thick, a yellowish basal layer of horizontal hyphae and an intermediate layer of variable thickness, clear yellow by transmitted light, which penetrates the spines, composed of indistinct agglutinated hyphae intermingled with crystalline accretions; hymenium continuous, covering both

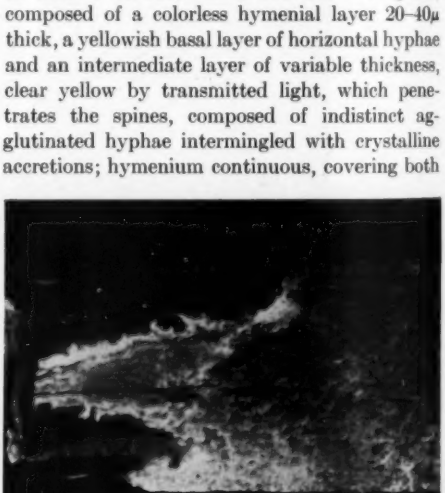


FIG. 1.—*Protodontia oligacantha*, type: Habit, × 1, showing fimbriate margin.

FIG. 2.—*Protodontia oligacantha*, type: Longitudinal section of spine, showing hymenium and sterile tip, × 80.

spines and area between them, except at tips of spines, composed of colorless basidia and dendrophyses; dendrophyses 3–4μ in diameter at base, branching subdichotomously several times and irregularly attenuated toward the tips, sometimes with clamp-connections; probasidia globose to ovate or pyriform, mostly 13–20 × 9–12μ, becoming cruciate-septate, each cell producing a thick, rather short epibasidium, 2–2.5(–3)μ in diameter; basidiospores cylindrical to allantoid, usually with numerous small guttules, sometimes with 1–3 large guttules and numerous smaller ones, (9–)10–12(–13) × (4–)4.5–5(–5.5)μ, germinating by repetition.

British Columbia: Cottonwood, August 3, 1949, W. G. Ziller, V-*5013* (DAOM *21881*), TYPE. Other collections examined: Cottonwood, July 26, 1949, M. K. Nobles, V-*5247* (DAOM *22974*); Cinema, August 11, 1949, W. G. Ziller, V-*5084* (DAOM *22973*) and V-*5087* (DAOM *21934*). All on dead wood of *Populus trichocarpa* T. & G. Numbers cited are those of Herb. Lab. For. Path. Victoria (V) and Myc. Herb. Sci. Serv. Dept. Agr. Ottawa (DAOM). Portions of all except V-*5084* are in Myc. Coll. S. U. I.

The specific epithet is based on ὀλίγος, few, and ἄκανθα, spine.

The outstanding characteristics of *P. oligacantha* are the sparse development of the spines and the broad, spineless, fimbriate margin (Fig. 1). Where most abundant, the spines number 3–5 to a square millimeter. They are fertile over most of the surface, as is the hymenium between them, but the extreme tip is often sterile (Fig. 2), owing to protrusion of an extension of the intermediate yellow layer, giving them a fimbriate appearance when examined dry under a binocular. They tend to be borne in lines on whitish strands, which makes the hymenial surface appear faintly reticulate under a lens. Some specimens of *Eichleriella spinulosa* (B. & C.) Burt bear tubercles on the hymenial surface which may approach in abundance the spines of *P. oligacantha*, but the much thicker, darker fructification, the larger spores and basidia and the strongly determinate margin of the former species mark it as clearly distinct. The basidia and spores are of approximately the same size as those of *E. macrospora* (Peck) Martin, which may bear scattered tubercles and is sometimes subfimbriate and indeterminate when young, but the thick, determinate fructification of mature collections of that species and the characteristic texture, difficult to describe, but readily recognizable when known, make it impossible to consider it the same as the Canadian fungus. In the four ample collections which have been studied, there is no suggestion that *P. oligacantha* ever develops a determinate margin. It seems probable, however, that collections made later in the season might show a somewhat more extensive development of the spines. The basidia and spores (Fig. 3) are characteristic of the Tremellaceae. There is often a suggestion of a clamp connection at the base of the basidium, but in most cases this cannot be seen. The dendrophyses (Fig. 3, *c*) are rather difficult to see since the terminal portion does not stain.

The largest fructifications examined were 13 × 4 cm and 12 × 5 cm respectively, one of

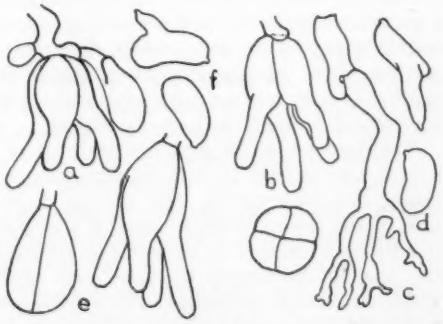


FIG. 3.—*Protodontia oligacantha*: *a–d*, no. *V-5087*. *a*, Two basidia and ovate structure, probably a very young basidium (note beak on basidium at right); *b*, two basidia, one in apical view; *c*, dendrophysis; *d*, two spores, one preparing to germinate by repetition. *e–f*, No. *V-5013*. *e*, two basidia, *f*, two spores, one preparing to germinate by repetition. All × 1,000.

these measurements secured by matching two broken pieces. The growth may well become much more extensive.

Some years ago (Mycologia **24:** 508–511. 1932) I discussed the genus *Protodontia* with particular reference to our commonest species, which I referred to *P. uda* v. Höhn., and at that time commented on the genus *Protohydnum* Möll., in which *Protodontia* is often included. Recently (Univ. Iowa Stud. Nat. Hist. **19** (3): 63. 1952), I reported *P. piceicola* (Kühner) Martin from Ontario. A collection from Louisiana by Langlois, determined by him as *Protohydnum lividum*, in the herbaria of the U. S. Dept. of Agriculture and the Missouri Botanical Garden, may well be that species and a *Protodontia*, but the generic transfer should be made only by one who has access to adequate European material. These seem to be the only species known from the United States and Canada.

Dr. M. A. Donk has been kind enough to let me see some of his notes on *Protodontia*. He believes that what I have referred to *P. uda* is in reality distinct from the European form. This may be correct. I have not seen enough European material to be certain it is not and have depended mainly on published descriptions for the determination of our collections. These, however, show substantial variation but nothing beyond what may, in my opinion, be considered as due to differences in degree of maturity or as responses to local environmental fluctuations. Whelden (Mycologia **29:** 100–115. 1937), who studied cytologically an American collection referred to *P. uda*, reports that his material had been compared with von Höhnel's type by Dr. D. P. Rogers, who found them to agree exactly.

ICHTHYOLOGY.—*Ten new American gobioid fishes in the United States National Museum, including additions to a revision of* Gobionellus. ISAAC GINSBURG, U. S. Fish and Wildlife Service. (Communicated by L. P. Schultz.)

During revisional studies of the genera of American fishes, the following 10 undescribed species and subspecies discovered in the U. S. Fish and Wildlife Service and the U. S. National Museum are here named and briefly described. All holotypes are deposited in the National Museum.

Figures of proportional measurements given below refer to percentages of the standard length. Lengths of the pectoral and ventral fins denote the length of their longest rays, from their point of articulation, as determined at the surface without dissection, to their distal margin. The given lengths of specimens refer to the total length, including the caudal fin, unless otherwise stated.

The numbers of fin supports are of paramount importance in the classification of fishes, including gobies. The precise structure of the fins of fishes in general, namely, the different kinds of fin supports comprising the fins, differs largely by family or other major taxonomic groupings. The variability and relative numbers of the different supports differ by species or population of lower rank, and also by higher taxonomic groups. The numbers of fin supports have been widely used in taxonomy; but the broader problem of the comparative morphology of the fins of fishes in general has been largely neglected. Lately, this subject began to engage the attention of investigators. Hubbs (Copeia, 1943: 134; 1945: 75) raises the question of the use of a certain fin formula in describing gobioid fishes, in connection with a discussion of the structure of the fins of other fishes. Beebe (Zoologica **27:** 45. 1942) is of the opinion that the last two approximated dorsal rays of *Dixonina*—a genus belonging to a different order than gobies—and related genera should be enumerated separately instead of counting them together as one ray. However, a thorough study of the comparative morphology of the fins in the major groups of fishes still remains to be made. As the fin structure differs largely by major groups, the proper and most advantageous method of enumeration, and any formula expressing such enumeration, will differ by such major groups.

In the superfamily Gobioidea the structure of the fins is as follows: The first dorsal consists of flexible (with few exceptions), unsegmented fin supports which are evidently homologous with the pungent spines of other fishes having two dorsal fins. The first fin support of the second dorsal is, as the fin supports of the first dorsal, likewise flexible and unsegmented, and is presumably also homologous with the pungent spine in

the same position of other fishes (although no thorough study has as yet been made to verify this assumption). The first unsegmented fin support of the second dorsal is followed by a variable number of segmented, and variously branched rays, the last two of which are very closely approximated at the base. The structure of the anal is the same as that of the second dorsal.

The above described structures apply to all the species in the superfamily and virtually to all the individuals of any species. Exceptions from the general rule that are now and then found in individual fish—and such exceptions comprise less than 1 percent of the combined counts of all the species examined—are to be considered as slight abnormalities rather than as representations of a normal individual variability. As these are superfamily characters, there seems no point in repeating these facts under each species, either in words or by a formula, as it is unnecessary to repeat any other superfamily character in the species descriptions. Consequently, in the descriptions here given the following uniform method is adopted in enumerating those rays that are of importance in separating the species: All counts are given in Arabic numerals. A semicolon separates the counts of the two dorsals and a hyphen connects the extremes of the range of the count of any given fin. The first unsegmented fin support of the second dorsal, and anal, is included in the count, while the last two approximated rays of both fins are counted as one. This is the method I used uniformly in previous publications on gobioids. If it is desired to get the number of segmented rays only, that is, to exclude the first fin support and count the last two as one ray, 1 is to be subtracted from the figures given below; to include the first and count the last two separately, 1 needs to be added; excluding the first and counting the last two separately, the numbers will be the same as those given below.

The rays in the pectoral fin of gobies generally do not differ in essential structure, except that some of the marginal rays grow progressively shorter, and the extent of branching decreases outwardly. In the following descriptions all the pectoral rays are included without distinction in the same count.

Family ELEOTRIDAE

Dormitator cubanus, n. sp.

D 7; 8–9. A 8–9. P 15. Sc 33–35. No mucous pores on preopercular sulcus. Total number of gill rakers in outer row of first gill arch, in a 94-mm specimen, 29. Head 30–31, postorbital part of head 15.5–16.5, caudal 27–28, ventral 23.5–24.5, pectoral 23–25.5. Body with a median longitudinal row of very diffuse spots; a dark shoulder spot above pectoral base; a dark, narrow, short, oblique band on cheek, under anterior margin of pupil to end of maxillary; the two dorsals and caudal with rows of small dark spots, roughly transverse on caudal and oblique on dorsals. (No oblique transverse light bands on body against a darker background as in related species, but their absence possibly due to fading.)

Holotype.—U.S.N.M. no. 55668. San Cristóbal, Cuba; C. H. Eigenmann; 1902; female 82 mm.

Paratypes.—U.S.N.M. no. 123234, a male obtained with the holotype, 73.6 mm in standard length with the caudal broken, approximately 94 mm in total length. U.S.N.M. no. 55688; Pinar del Río, Cuba; C. H. Eigenmann; March 1902; female 48 mm.

Remarks.—This is a well-marked species and differs sharply from its congeners in the number of gill rakers. Specimens of comparable size, with that stated above, of the other species have a total of 51 or more gill rakers in the outer row of the first gill arch. It also differs in lacking pores on the preopercular sulcus, and in averaging fewer dorsal and anal rays and shorter fins; although there is more or less intergradation in these latter characters. Taking its character pattern as a whole, *cubanus* is sharply defined and rather easily distinguishable. It is probably a highly localized species and confined to some fresh-water streams in Cuba, as 445 specimens of *Dormitator* examined from the western Atlantic coasts, ranging from Texas to Brazil, and from several West Indian Islands including Cuba, all belong to the common Atlantic species, *maculatus*.

The three specimens forming the basis of this account were collected by Eigenmann (Bull. U. S. Bur. Fish. **22** (1902): 211–236. 1903) during his investigation of the cave inhabiting fishes of Cuba, in 1902, when he made many striking discoveries. He then obtained both *maculatus* and *cubanus* and recorded them together under the former designation.

Dormitator latifrons mexicanus, n. subsp.

D(6) 7 (8); (8) 9–10. A (9) 10–11. P 14–16. Sc 34–36.—Preopercular sulcus with pores, usually 4 in number. Total number of gill rakers in outer row of first gill arch, in 3 specimens 242–256 mm (from Colima, Mexico), 132–145, and in the same specimens, head 30.5–32.5, postorbital 16–18, caudal 30.5–32.5, ventral 20–22, pectoral 22.5–24. In the holotype, gill rakers 107, head 33, postorbital 19, caudal 34.5, ventral 21.5, pectoral 25.5. Body dark with rather narrow, obliquely transverse, diffuse, lighter cross bands; a large very dark shoulder spot near and over pectoral base; a narrow dark band on cheek under anterior margin of pupil to end of maxillary; posterior part of head with dark longitudinal, nearly parallel bands, rather faint to well defined; a somewhat curved band at pectoral base.

Holotype.—U.S.N.M. no. 7350. San Lucas, Lower California; I. Xanthus; male 140 mm.

Remarks.—Other 49 specimens 24–256 mm examined from the Pacific coast of Mexico ranging from La Paz in the Gulf of California to Salina Cruz in the gulf of Tehuantepec.

The subspecies *mexicanus* differs from *latifrons* chiefly in the number of gill rakers and the head length. Both of these characters differ also intraspecifically with the size of the fish and it is necessary to compare specimens of like size. Two specimens of *latifrons* from the Pacific coast of Panamá, 235–259 mm, comparable in size with the large specimens described above, have gill rakers 149–164 and head length 33.5–38. *D. mexicanus* also averages a shorter caudal, ventral, pectoral and postorbital part of the head; but it intergrades considerably with *latifrons* in these characters. The two are apparently allopatric populations on the Pacific coast of Mexico and Central America, respectively. In this preliminary account the few largest specimens are compared and they do not show intergradation in the two chief characters. However, a comparison of the 50 specimens examined of *mexicanus* with 47 specimens of *latifrons*, segregated by comparable size groups shows that they intergrade with a degree of divergence of subspecies magnitude.

The name *latifrons* was proposed by Richardson for two specimens from the "Pacific Ocean." It has since been used for the common eastern Pacific species of *Dormitator*, including Mexico and Central America, or the name was placed in the synonymy of *D. maculatus*, depending on whether an author treated the eastern Pacific population as a distinct species, or he treated that population as being conspecific with that from the western Atlantic. As the common eastern Pacific species is here divided into two subspecies, the name *latifrons* is hereby restricted to the Panama population, since it is more likely that Richardson's specimens came from the coast of central America than that of Mexico.

Guavina micropus, n. sp.

D 7; 10. A 10. P 16. Sc 89. Almost completely scaled, except underside of head, and preopercular sulcus, and a small area on side of snout in front of eye, altogether or largely scaleless. Scales on posterior part of body rather weakly spinulose, others cycloid. Ventral 11.5, pectoral 16, body depth 22.5, least depth of caudal peduncle 15, head 31, postorbital 18, head depth directly behind eye 15, head width at same point 20, maxillary 13, snout 9, eye 5.5, interorbital 10.5, antedorsal distance 36.5. Color brownish, dark on dorsal aspect, much lighter below; no saliently distinctive markings, pigment somewhat concentrated on upper part of pectoral base forming a rather faint, diffuse blotch.

Holotype.—U.S.N.M. no. 123230. Miraflores Locks, Panama Canal; east chamber; A. O. Foster, April 28–29, 1937; female 90 mm in standard length, the caudal damaged.

Remarks.—Only one species of this genus was known heretofore, *G. guavina* from the western Atlantic coasts. The new species differs at a glance in having a strikingly short ventral fin, which also shows up well after measuring, 10 specimens of *guavina* having the ventral 18–19.5. This species also has a shorter pectoral and antedorsal, but these differences are not as great as that of the ventral; in the same 10 specimens of *guavina*, pectoral 20.5–22, antedorsal 39.5–41.5. It also has one ray less in the dorsal (in the specimens examined of *guavina*, the dorsal rays are constantly 11), and it further differs in having the preopercular sulcus naked instead of scaled over.

This is most probably a hitherto undiscovered Pacific species, corresponding to the Atlantic *guavina*, which has found its way into the Panama Canal.

Gobiomorus polylepis, n. sp.

D 6; 10. A 10. P 18. Sc 77–78. Caudal 24.5,

ventral 18.2–18.4, pectoral 17.8–18, depth about 20 (belly collapsed and not accurately determinable), peduncle 11.5–12, head 30–30.5, postorbital 18–18.1, head depth 12.3–12.4, head width 14.7–14.8, maxillary 12.5–13, snout 9.5–10, eye 3.4–3.8, interorbital 7–7.5, antedorsal 36.5–37. Irregularly shaded, without distinctive markings (perhaps faded from long immersion in preservative); pectoral, caudal and the two dorsals with rows of small diffuse spots.

Holotype.—U.S.N.M. no. 130917. Colima, Mexico; exhibited by Mexican Government at Chicago World's Fair, 1893; female 277 mm, 222 mm in standard length.

Paratype.—U.S.N.M. no. 123233; from same container as the type; female 243 mm in standard length with caudal end broken off, approximately 303 mm in total length.

Remarks.—Two common and widespread species of *Gobiomorus* were known heretofore, *maculatus* from the Pacific drainage and *dormitor* from the Atlantic drainage. In preparing a revision of the genus, *polyelpis* was compared with 257 specimens of *maculatus* from localities ranging from the Gulf of California to Peru, including 14 specimens from the coast of Mexico, and 204 specimens of *dormitor* ranging from Texas to Venezuela. This is a strongly marked species and is easily distinguishable from the two common species by the number of scales. In 175 specimens of *dormitor* the range of the scale count is 58–64, in 241 specimens of *maculatus* the range is 54–60, as compared with 77–78 in *polylepis*. In the number of anal and pectoral rays, *polylepis* nearly agrees with the Atlantic *dormitor*, rather than with the Pacific *maculatus*, and in the number of scales it is also nearest *dormitor*. It is remarkable that such a sharply defined and large gobioid species from the North American continent escaped detection up to now. It is probably another one of those species having a narrowly circumscribed geographic range.

Erotelis smaragdus civitatum, n. subsp.

D 6; 12. A 10. P 17. Sc 105. Scales on dorsal aspect extending to within a short distance of eyes; opercle entirely scaleless; cheek almost naked, only a few scales present posteriorly near its middle; all scales cycloid. Preopercular spine rather reduced and concealed under the skin. Caudal 27.5, ventral 13, pectoral 15.5, depth 15, peduncle 10, head 20.5, postorbital 13.5, head depth 9, head width 9.5, maxillary 7.5, snout 4.2, eye 3.2, interorbital 4.3, antedorsal 32.5. Color almost uniformly dusky, darker on dorsal and somewhat lighter on ventral aspect; pigment somewhat concentrated on upper part of pectoral base to form a diffuse blotch; otherwise no distinctive color marks.

Holotype.—U.S.N.M. no. 123229. St. Vincent Island, Fla.; taken with seine in deep soft mud in large pond on the bay side of the island; Isaac Ginsburg; July 23, 1932; female 123 mm.

Remarks.—The above description is drawn from the holotype. Two small specimens 46–57 mm from Harbor Island, Tex., collected by John C. Pearson, have the following counts: D 6; 12. A 10. P 18. and D 6; 11. A 10. P 17.

This subspecies differs from *smaragdus* chiefly in the number of dorsal rays. In 26 specimens of *smaragdus* the dorsal rays number 11 in 25 and 10 in 1. In 11 specimens of the Pacific *armiger* the dorsal rays number 13 in 9 and 12 in 2. The dorsal count in *civitatum*, 12 in 2 specimens and 11 in 1, is intermediate between *smaragdus* and *armiger*. While only 3 specimens of *civitatum* are available, fair composite samples of *armiger* and *smaragdus* were examined to show that it diverges at least subspecifically from the latter. The samples examined indicate a divergence of subspecies degree. In general appearance, *civitatum* is not as excessively slender as *smaragdus* which is almost anguilliform, but somewhat approaches in this respect the species of the closely related genus *Eleotris*. This difference is rather marked on direct comparison of specimens, but does not show up well in measurements.

Of the 26 specimens of *smaragdus* examined 7 are from Key West, the others are from Cuba, Haiti, Puerto Rico, Curaçao, Panamá, and Venezuela. Consequently the Key West population of *smaragdus* is nearer to those of the West Indies and Central America than to that on the northern Gulf coast of the United States.

Chriolepis tagus, n. sp.

D 7; 12. A 11. P 19. Anterior part of body naked, posterior part scaled, scales extending forward to under end of first dorsal; caudal base with modified scales. (The single specimen described is in but indifferent condition, the squamation especially is defective and nearly all scales have fallen. The scale pockets indicate the extent of squamation. On the caudal base only one scale is now remaining, at its outer angle, a conspicuously modified, large ctenoid scale, very similar to the scale present in *Chriolepis minutillus* in the same position.) Lower jaw with

two inner posterior caninoids. Eye large, the interorbital narrow. Ventral falling considerably short of anus. Pectoral reaching beyond a vertical through origin of first dorsal. Tongue moderately emarginate. (Color apparently faded, only a few large scattered chromatophores on head.)

Holotype.—U.S.N.M. no. 123232. Tagus Cove, Albemarle Island, Galápagos Archipelago; dredged in 10–18 fathoms; Hancock Expedition, W. L. Schmitt; January 15, 1934; male 16.3 mm in standard length, 21 mm to end of partly broken caudal.

Remarks.—The squamation is more extensive in this species than in any known species of *Chriolepis*. The number of anal and pectoral rays is higher than in any other species. The number of dorsal rays is higher than in any species, except some individual variants of *minutillus*. Altogether, *tagus* is a sharply divergent and strongly marked species.

Chriolepis benthonis, n. sp.

D 7; 9. A 8. P 16. Anterior part of body naked, posterior part scaled; scales extending forward to a point near midline under base of seventh dorsal ray; in 12 oblique rows to base of caudal; a few scales on posterior part of peduncle ctenoid, most scales cycloid; modified scales on caudal base present (most modified scales missing and cannot be described in detail). Lower jaw without posterior inner caninoids. Eye very large; interorbital very narrow. Ventral reaching anus. Pectoral reaching to under base of first dorsal ray. Tongue entire. Ventral 28.5, pectoral 27.5, depth 21, peduncle 12, head 30.5, postorbital 14.5, head depth 17, head width 19, maxillary 12, snout 8, eye 10.5, interorbital 2, antedorsal 37.5. (Color a rather uniform light yellowish, probably faded.)

Holotype.—U.S.N.M. no. 47641. *Blake* Expedition, station CCXLI, Alexander Agassiz; off Progreso, Yucatán, Mexico; lat. 23° 13′ N., long. 89° 10′ W.; 84 fathoms; male 30.7 mm in standard length, the caudal damaged.

Remarks.—This species has the lowest number of dorsal and anal rays of any known species of *Chriolepis*. The extent of scalation is nearly as in the Pacific *zebra*; it differs from that species, besides the difference in the number of dorsal and anal rays, also in having smaller teeth, a larger eye and narrower interorbital.

Psilotris, n. gen.

Genotype.—Psilotris alepis, n. sp.

This genus is characterized by and differs from all known American eleotrid genera, by a combination of two characters: the total lack of scales and the absence of mucous pores. Full grown specimens of *Eleotrica* also lack scales; but *Psilotris* differs in lacking pores as well. A detailed study of American gobioids leads to the conclusion that the character of the pores is more important as a phylogenetic criterion than the character of the squamation. It follows then that *Psilotris* is more nearly related to *Chriolepis* which also lacks pores, although the latter has the body partly scaled. With respect to the squamation, and other characters as well, *Psilotris* and *Chriolepis* present a closely analogous, parallel development to the genera *Gobiosoma* and *Garmannia* in the family Gobiidae.

Etymology.—Psilotris, an abbreviated form of psiloeleotris (naked eleotris).

Psilotris alepis, n. sp.

D 7; 10. A 9. P 15. Scales altogether absent, on caudal base as well as on the body and head. Body moderately elongate, compressed; head moderately depressed. Maxillary ending under anterior margin of pupil. Mouth subterminal, lower jaw but slightly projecting; gape very moderately inclined, a horizontal through distal margin of upper lip passing through lower part of eye. Teeth in bands; outer teeth well enlarged; inner posterior teeth in lower jaw also enlarged, but hardly large enough to be described as caninoid. Ventral falling considerably short of anus; pectoral slightly short of a vertical through base of first dorsal ray. Gill opening restricted, attachment of branchiostegal membrane near lower part of pectoral base. Female anal papilla large, thick, globose. No mucous pores on head. Caudal 27.5, ventral 23.5, pectoral 27.5, depth 23.5, peduncle 13.5, head 30.5, postorbital 18, head depth 16, head width 17.5, maxillary 11.5, snout 7, eye 7, interorbital 3, antedorsal 42.5. (Because of the very small size of the specimen measured, and the comparative crudeness of the instrument used, an ordinary Vernier caliper, the preceding measurements are rough approximations only.) Diffusely cross-banded; body with 5 broad, irregular, diffuse bands, the anterior 2 somewhat Y-shaped; a subvertical, diffuse band under anterior part of eye; a wider, oblique band under posterior part of eye.

Holotype.—U.S.N.M. no. 123231. St. Croix Island, Virgin Islands; on reef; Smithsonian Hartford Expedition, W. L. Schmitt; April 8, 1937; female 17 mm. The small specimen examined appears to be an adult. It apparently represents a very small species, rather than the young of a larger species.

This species is readily distinguished from all known western Atlantic eleotrids by its total lack of scales. Its relationship is discussed above under the genus account.

Family GOBIIDAE

Genus **Gobionellus** Girard

Since my revision of this genus was published (Bull. Bingham Oceanogr. Coll. **4** (art. 2). 1932), I had the opportunity to study many more samples of nearly all species, comprising for most species many more specimens than those forming the basis of the revision. Besides the additional specimens examined, characters hitherto generally neglected and not considered in the revision, have been studied in detail. The more striking results of this study of additional samples and characters are as follows: (1) Two new species were discovered. (2) It was concluded that two American species, previously described and referred to *Euctenogobius*, are more properly placed in *Gobionellus* as their character pattern, in general, fits in well with the other species of the latter genus. (A discussion of the status of *Euctenogobius* has been published by me in Proc. U. S. Nat. Mus. **82:** 19. 1933.) (3) The relationship of one species as treated in the revision, needs emendation. The two new species are here described, and also three new subgenera are established, in accordance with the additional information to place all species in their proper place in the scheme of classification employed in the revision.

Gobionellus mystax, n. sp.

D 6; 13. A 14. P 17–19. Sc 70–73. Scales extending on antedorsal area to a vertical plane through preopercular sulcus, a narrow naked area on midback, corresponding to predorsal keel, extending from origin of first dorsal, all the way forward; dorsal area in front of preopercular sulcus, and side of head scaleless; throat largely naked, except a rather narrow longitudinal median strip of scales; pectoral base scaleless; ventral aspect of belly scaled, except a rather moderate naked area directly behind base of ventral fin; anterior scales and those on belly cycloid, posterior scales nearly all ctenoid, the ctenoid scales beginning at a point near midline under base of fourth dorsal spine. Teeth in narrow bands, those in outer and inner rows only a little larger than others. Second and third dorsal spines in male notably prolonged, the third longest, reaching base of fifth dorsal ray. Maxillary notably long, its end reaching preopercular margin or nearly so. Caudal 55.5–57.5, ventral 20.5–21, pectoral 19, depth 16–17, peduncle 9–9.5, head 22, postorbital 10.5–11, head depth 13, head width 11–11.3, maxillary 15.5–16, snout 8–8.5, eye 4.5, interorbital 3.5–4, antedorsal 29. (Color dark all over without distinctive markings, probably the color pattern obliterated from long immersion in preservative.)

Holotype.—U.S.N.M. no. 130859. Laguna de Mexcaltitan, Territory of Tepic [now the state of Nayarit], Mexico; exhibited by Mexican Government at Chicago World's Fair, 1893; male 227 mm, 144 mm in standard length.

Paratype.—U.S.N.M. no. 123235. In same lot with the type; male 251 mm, 161 mm in standard length.

Remarks.—This species is close to *microdon* and belongs in the same subgenus with it, *Gobatus*. It differs in having a longer maxillary and caudal. In the genus *Gobionellus* both of these characters differ with the species and also intraspecifically with sex and size, the caudal considerably and the maxillary moderately so. As the two specimens examined are very large males, it may be suggested that the seemingly specific differences are rather due to their size and sex. However, they were compared with a male of *microdon* 117 mm in standard length from Miraflores Lake, Panama Canal, not much smaller than the two specimens here described, and the differences in these two characters are too pronounced to be reasonably ascribed to intraspecific individual variability or sex and size differences. They are evidently interspecific differences and the two specimens represent a species close to but different from *microdon*. In the above male of *microdon*: caudal 34; maxillary 12.5, ending under posterior margin of eye. The maxillary in *mystax* is so strikingly long that the generic definition given in my revision of the genus needs to be emended to include this species.

The scales in the two specimens of *mystax* number 70–73, while in the two types of *micro-*

don from Río Ahome, México, they number 60–61, and it would seem that the two species also differ in the scale count. However, in two specimens of *microdon* from Río Juan Diaz, Panamá, the scales are 59–65, while in two from the Panama Canal they number 69–72. Consequently, the scale count in *microdon* seems to differ intraspecifically with the population, and its possible value as an interspecific character remains to be determined by more extensive samples.

Gobionellus gracillimus, n. sp.

D 6; 14. A 15. P 18–20. Sc 83–99. Antedorsal area completely scaled to within a short distance of eyes; opercle with a moderate-sized patch of scales at upper anterior corner; cheek naked or a few scales present; throat partly scaled; pectoral base scaleless; ventral aspect of belly scaled over posteriorly, a rather large or moderate sized area behind base of ventral fin naked; anterior scales cycloid, posterior scales mostly ctenoid, the ctenoid scales beginning at a point variably situated under base of third dorsal spine to under base of fifth dorsal ray. Teeth in narrow bands, those in outer and inner rows a little larger than those in between. Maxillary generally ending under space between posterior margin of pupil and that of eye, slightly past eye in the largest males. Second to fourth dorsal spines notably prolonged in large specimens, the longest spine usually reaching to base of fifth or sixth dorsal ray, sometimes to base of third ray. Body notably slender and caudal notably long; depth 11.9–15.5 in female, 11–13.3 in male; caudal 41–46.5 in female, 51.5–63.5 in male. Other measurements not of paramount specific importance and only slightly or moderately different with sex, the range of both sexes as follows: ventral 17.5–21.5, pectoral 16.0–20.5, peduncle 7.5–9, head 18–21.5, postorbital 8.5–11.5, head depth 10.5–13, head width 9–10.5, maxillary 9.5–11.5, snout 6.5–7.5, eye 3.5–5, interorbital 2–3, antedorsal 25–29.5. (All preceding measurements, including that of caudal and depth, of specimens 106–165 mm in standard length.) A large, longitudinally oblong, dark spot below first dorsal and centered slightly above middle of body; a small spot on caudal base; 2 or 3 small dark spots on anterior margin of first dorsal; a median longitudinal row of many small spots, well marked in a recently preserved specimen, now faded, and not discernible in other preserved specimens; the large body spot and the caudal spot rather well marked in the smaller specimens, faint or imperceptible in large ones (color pattern seemingly becoming faint with growth and also fading in preserved specimens).

Holotype.—U.S.N.M. no. 123227. Apalachicola Bay, Fla.; trawl; July 16, 1932; Isaac Ginsburg; male 271 mm, 165 mm in standard length.

Remarks.—Thirteen other specimens 106–157 mm in standard lengths were studied from St. Johns River, New Smyrna, and Pensacola Bay, Fla.; Bayou St. Denis, La.; off Padre Island, Tex.

In the revision of the genus, the populations of the extremely long bodied, western Atlantic gobies which belong to the subgenus *Gobionellus*, were divided into two species on the basis of the scale count, *hastatus* with more numerous scales from the northern Gulf coast, and *oceanicus* with fewer scales from Key West, the West Indies, and Central America. On the basis of the samples examined for the revision of the genus, the two species showed both a morphologic and geographic gap between them. Hildebrand and Cable later found that their geographic ranges overlap and that both species occur at North Carolina (Bull. U. S. Bur. Fish. **48:** 365. 1938). By an examination of many more specimens, I now find that these two species also intergrade somewhat in the scale count and are not as easily separable as the smaller samples indicated. Furthermore, I now find that the finer scaled gobies from the coast of the United States (58 specimens were now examined instead of the 7 specimens examined for the revision), fall into two groups, rather roughly separable by four correlated characters. One group, here distinguished as *gracillimus*, has a longer caudal, more slender body, longer dorsal spines and more numerous scales. The data for the four characters seem to form four bimodal curves, and we are evidently dealing with two distinct populations, *gracillimus* and *hastatus*. However, they intergrade in all four characters and individual specimens cannot always be placed with certainty. If a specimen has all four, or at least three, of the characters typical or close to the mode of its population, it can be placed with a measure of assurance, and this is so with the large majority of specimens. But, if a specimen has less than three characters correlated, or if three or four of its characters fall near the borderline its proper position is doubt-

ful. (Such doubtful specimens constitute approximately 10 percent of the total.) Consequently, the proper taxonomic status of these two evidently distinct populations is uncertain. If they were to occupy separate geographic ranges, they should properly be treated as two geographic subspecies, and such a course could hardly be questioned. As it is, they either constitute two coordinate, synpatric subspecies, in which case they form an exception to the general rule that two subspecies occupy separate territories, perhaps they are ecological subspecies having nearly the same geographic range; or they constitute two full species which are but incompletely distinguishable by current taxonomic methods. These questions might be resolved by a more elaborate sampling of the populations, perhaps supplemented by ecological studies. The distinguishing characters, except the scale count, differ also with size and sex, and hence it would take very extensive samples to work out the finer details.

Large males, 120 mm or over in standard length, diverge most, and such specimens are well separable by species.

It is probable that depth of water is a factor in the distributional basis of the separation of the two species. Detailed records of capture are wanting or incomplete for most of the constituent samples examined. But judged by the available records, it seems that *gracillimus* is usually taken with a trawl, while *hastatus* is taken with a seine as often as with a trawl. However, neither species is a real deep water fish. The greatest depth recorded is 10 fathoms for a specimen of *gracillimus* taken off Padre Island, Tex. Eight of the 14 specimens of *gracillimus* examined, comprising 5 constituent samples, were taken in Pensacola Bay and that body of water seems to be the center of distribution of the species.

Gobidus, n. subgen.

Genotype.—*Gobionellus longicaudus* (Jenkins and Evermann) = *Gobius longicaudus* Jenkins and Evermann.

Before this subgenus is characterized, two new symbols are herewith proposed to be used for two mucous pores placed over the opercle. In Sanzo's (Mitth. Zool. Stat. Neapel **20:** 251–328. 1911) system of symbols for the various parts of the lateral line organs of gobies, the anterior and posterior pore which form the openings of the mucous channel over the opercle, are designated as ρ' and ρ'', respectively. His symbols for these pores are rather cumbersome, somewhat confusing, and to a certain extent misleading in that those two pores are often present or absent independently of ρ, at least I find it so in the American species. The symbols θ and τ are, therefore, here proposed to designate the anterior and posterior pore, respectively.

Extreme groups of species of *Gobionellus* are sharply distinguished by three striking characters, in addition to others. Those of the subgenus *Gobionellus* have a notably long and slender body, small scales, and they possess θ and τ; while those of *Gobica* have a body more like the usual gobiid shape, large scales and they lack θ and τ. The subgenus *Gobidus* lacks θ and τ like *Gobica*, its scales are nearly as in *Gobionellus*, while the body shape is rather intermediate or nearer to *Gobionellus*. Its dorsal spines are not at all prolonged and shorter than in any other subgenus, except *Congruogobius*. In the revision, the species of this subgenus was included with *microdon* in the subgenus *Gobatus*, largely on the basis of the scale and fin ray counts. However, the latter has θ and τ, and in other characters as well is much nearer the subgenus *Gobionellus*. *Gobidus* essentially agrees with *Gobica* in the lateral line organs and the color pattern, and in spite of superficial appearances, it is nearer to that subgenus than to *Gobatus*.

Gobionellus longicaudus has generally been placed by authors in the synonymy of *sagittula*, and in the revision of the genus I disposed of that name in the same manner; but the study of additional samples and characters show that the Mexican *longicaudus* and the Panamanian *sagittula* diverge markedly in the number of pectoral rays (a character not studied in detail in the revision) and scales, although they intergrade to some extent and may perhaps be treated as coordinate geographic subspecies. Without a definite commitment as to the taxonomic rank of *longicaudus* for the present, I prefer to designate it as the genotype of *Gobidus* because I have examined the type specimens and am certain of its position, while *sagittula* I identify only from its description.

Gobatinus, n. subgen.

Genotype.—*Gobionellus panamensis* (Meek and Hildebrand) = *Euctenogobius panamensis* Meek and Hildebrand.

This subgenus also is in a sense intermediate between the two groups noted above in that it has a combination of important characters of both groups, but in a manner reverse from that of the subgenus *Gobidus*. The scales are large (34–37) as in *Gobica*, while it has θ and τ like *Gobionellus*. The body shape is intermediate between that of the last two named subgenera. *Gobatinus* has the teeth in the upper jaw usually in one row; sometimes a second incomplete inner row is present. In the other subgenera, the teeth in the upper jaw are in 2–5 rows, depending on the subgenus.

Congruogobius, n. subgen.

Genotype.—Gobionellus liolepis (Meek and Hildebrand) = *Euctenogobius liolepis* Meek and Hildebrand.

This subgenus differs from all others in having the two dorsal fins confluent and the scales cycloid, except that the scales on a narrow strip along a median area on the posterior part of the body are weakly ctenoid or cycloid. In these two characters it is somewhat intermediate between the genera *Gobionellus* and *Gobioides* but much nearer the former. Indeed, *Gobionellus* and *Goboides* are nearer in relationship than has been heretofore suspected. This is shown not only by the somewhat intermediate positions occupied by the subgenus *Congruogobius*, but by other characters as well, especially by the lateral line organs, a discussion of which would take us too far afield here. The scales in *Congruogobius* are 77–84; θ and τ are present. In the latter two characters, as well as in the shape of the body and the number of fin rays, it nearly agrees with or is nearest to the subgenus *Gobionellus*. The interorbital is rather wide as in the subgenus *Gobionellus*, while the eye is even smaller than in that subgenus when specimens of the same size are compared. In the latter two characters it also somewhat approaches *Gobioides*.

MALACOLOGY.—Amnicola brandi, *a new species of snail from northwestern Chihuahua*. ROBERT J. DRAKE, Biblioteca y Museo de Sonora, Hermosillo, Sonora. (Communicated by Joseph P. E. Morrison.)

In the middle of April 1949, the writer was in northwestern Chihuahua with Prof. C. Clayton Hoff, of the Department of Biology of the University of New Mexico. At that time, Dr. Hoff was the recipient of a grant-in-aid from the United States Public Health Service for collecting and studying ectoparasites (fleas and lice) of rodents in northern Chihuahua and southern New Mexico. During this trip, at Las Palomas, Distrito Galeana, Chihuahua, the type material of the species of fresh-water amnicolid snail here described was collected. The Las Palomas region is the type locality of another amnicolid, described as *Bythinella palomasensis* by Henry A. Pilsbry (1895: 68–69; Dall, 1898: 369–370). He based his description on two dead shells that had been collected in April 1892 by Edgar A. Mearns, military medic and naturalist of the International Boundary Commission of the United States and Mexico. Mearns, assisted by Frank X. Holzner, made daily collecting visits to Lake Palomas during the period from April 7 to April 15, 1892. (Mearns, 1907: 10). In the description of *Bythinella palomasensis*, Mearns's locality was given as merely at "Lake Palomas, northeastern [sic] Mexico."

Lake Palomas in northwestern Chihuahua, as it normally existed in the later 1800's, is no more. Then it consisted of a chain of shallow and marshy ponds connected by a small running stream, all of which terminated in a more or less broad and shallow permanent lake. The area of the old lake bed now fills with water only during the short rainy season; otherwise, it is a dusty and waterless flat.

The small town of Columbus, Luna County, N. Mex., is on the border. The small Mexican port-of-entry and customs station at Palomas, Chihuahua, is 1 mile south of Columbus. Las Palomas is a small collection of adobe houses 6 miles south of Palomas and the border. It is at Las Palomas, Chihuahua, that "some fine, bold springs" as noted in the International Boundary Commission report (1898, pt. II: 16) are located. The species of Amnicolidae described, lives in the Las Palomas springs with another amnicolid (undetermined, perhaps a *Lyrodes*), the common pea-clam *Pisidium abditum* Haldeman, and

a form of the everpresent *Physa*. No shells belonging to the present new species were found that remotely resemble the single illustration of the moderately high and narrow *Bythinella palomasensis* Pilsbry (Dall, *loc. cit.*, pl. 31, fig. 9).

The region was very dry at the time of our 1949 trip; no land shells were found alive or aestivating. Some shells were gathered from the *rejectamenta* of the Rio Casas Grandes at the Vado de Fusiles about 30 miles due south of Palomas and the border. They will be reported on in time.

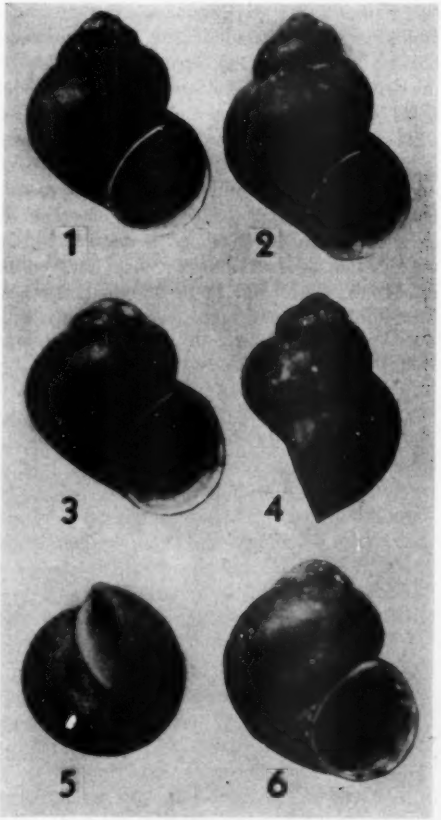
Dr. Harald A. Rehder, curator, Division of Mollusks, U. S. National Museum, kindly provided illustrations of the type material for this paper. Dr. Joseph P. H. Morrison, of the same division, gave much help in many ways.

Amnicola brandi, n. sp.
Figs. 1–6

Holotype.—The shell is white, under average size for genus, and globose. The spire is short and rounded; the protoconch is elevated and slightly eroded. The umbilicus is deeply perforate and narrow. The surface exhibits very faint growth wrinkles. There are 3.9 whorls which are convexly inflated and have some shouldering at the moderately impressed sutures. The aperture is oval, wider than high; its height and width equal about half the height and width of the entire shell. The inner lip flares slightly, is very white, and its callus forms a rounded rim on the side next to the umbilicus. The holotype (U.S.N.M. no. 601494) measures: length, 2.2 mm; width, 1.8 mm; aperture length, 1.0 mm; aperture width, 1.0 mm. It was collected by C. Clayton Hoff and Robert J. Drake, on April 15, 1949, in springs at Las Palomas, Chihuahua.

This species is named in honor of Dr. Donald D. Brand because of his long period of active interest in the geography, archeology, and natural history of northern Mexico—especially that of northwestern Chihuahua. Brand's archeological writings are so steeped in geographic description that his works on northwestern Mexico are indispensable references for naturalists and anthropologists interested in study of the area (see especially Brand, 1935, 1936, 1937, 1943).

Paratypes: The five descriptional paratypes (U.S.N.M. no. 601495) are illustrated (Figs. 2–6). About 200 paratypes were collected. They have been deposited as follows: Wendell O. Gregg Collection, 5132; Academy of Natural Sciences of Philadelphia, 185402; Ernest J. Roscoe Collection, 295; Morris K. Jacobson Collection, 2257; Department of Paleontology of the California Academy of Sciences, 32878; Allyn Hancock Foundation of the University of Southern California, 1230; Carnegie Museum, 62.39827; Chicago Natural History Museum, 32001; Museum of Zoology of the University of Michigan, 169876; Drake Molluscan Collection, 1459, 1460; Museum of Comparative Zoology, 185251; Department of Geology Museum of the University of New Mexico, 1347; Elmer G. Berry Collection; Laboratory of Conchology of the Biblioteca y Museo de Sonora; Stanford University Paleontological Type Collection, 8025;



FIGS. 1–6.—*Amnicola brandi*, n. sp.: 1, Holotype (U.S.N.M. no. 601494): 2–6, paratypes (U.S.N.M. no. 601495).

American Museum of Natural History, 72857; S. S. Berry Collection; Joshua L. Baily, Jr., Collection; Museum of Paleontology of the University of California, 36121–36129; San Diego Society of Natural History; Allyn G. Smith Collection, 9027; Hans Friedrich Collection, 9936; U. S. National Museum, 600499, 600500.

Discussion.—Amnicola brandi is a species that is small in size when compared with most of the amnicolids of the eastern United States and Canada. This feature is shared in common by all Southwestern Amnicolidae. Consistency of characters is evidence for long isolation and "inbreeding" for the species. Dr. Joseph P. E. Morrison (1949) has presented a classification of the subfamilies of the Amnicolidae based primarily on reproductive features. These four subfamilies are: Hydrobiinae, Bythinellinae, Buliminae, and Emmericiinae. Dr. Morrison has examined the male organs of some of the preserved paratypes of *Amnicola brandi*. He reports *brandi* has only one functional duct in the male reproductive system. Therefore the species is placed generally in the Hydrobiinae. (The operculum is paucispiral with the concave side next to the animal.) The genus of *brandi* is closest to what is considered *Amnicola* s. s. In time, a new generic category may have to be established for *brandi*. To do so now and before Morrison's results of many years of study with the family are available to all concerned would only be confusing. Many species that have been placed in *Amnicola* very probably belong in "*Amnicola*" and consequently in any of the subfamilies now recognized as biological.

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